

Temperature-Dependent Development and Oviposition Behavior of *Trichogramma ostrinae* (Hymenoptera: Trichogrammatidae), a Potential Biological Control Agent for the European Corn Borer (Lepidoptera: Crambidae)

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ABSTRACT *Trichogramma ostrinae* Pang and Chen (Hymenoptera: Trichogrammatidae) was reared continuously for seven generations on its native host, the Asian corn borer, *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae). It took 6.7 d at 33°C and 20 d at 17°C from oviposition to adult emergence with no differences between sexes. Several theoretic models were used to fit the temperature-dependent growth curves of *T. ostrinae*. A transformed day-degree model and the Hilbert-Logan model were the most reliable for predicting temperature development of *T. ostrinae*. The wasps reared on *O. furnacalis* at 27°C by the seventh generation had a lower level of parasitism than wasps from other generations and at other temperatures (17–33°C). The number of wasps emerged from individual parasitized egg, and percentage of females produced did not differ for any generations and temperatures. The differences among different generations for the amount and proportion of time female wasp spent drumming host eggs did not show any host- and generation-related trends. The time spent drumming by *T. ostrinae* female wasps reared for three generations on *O. furnacalis* and then four and six generations on the rice moth, *Corcyra cephalonica* (Stainton), differed slightly from the other generations. High variability among the tested wasps indicated that a large number of replicates would be needed to detect the probable differences among generations.

KEY WORDS *Trichogramma ostrinae*, *Ostrinia furnacalis*, temperature-dependent development, model, oviposition behavior

USE OF DIFFERENT *Trichogramma* species to control lepidopteran pests has been practiced in many countries, although most applications involved only five *Trichogramma* species against major pests, *Ostrinia spp.* and *Helicoverpa zea* (Boddie). At least six *Trichogramma* species have been used around the world to control *Ostrinia spp.* (Li 1994, Smith 1996). Among them, *T. nubilale* Ertle and Davis is considered to be the most suitable candidate for controlling the European corn borer, *O. nubilalis* (Hübner), in the United States (Losey and Calvin 1991), and *T. ostrinae* for the control of the Asian corn borer, *O. furnacalis*, in China (Zhang 1988, Zhang et al. 1990). Commercially available *T. brassicae* Bezdenko (= *T. maidis* Pintureau & Voegelé) was also evaluated for control of *O. nubilalis* on sweet corn and reduced 9–17% ear damage (Mertz et al. 1995). However, until recently, it was not possible to mass-produce *T. nubilale*. *T. ostrinae* was

brought from Jilin province of northeastern China into the United States for further evaluation to control the European corn borer because the two species of corn borers have the similar biologies, and studies have shown that *T. ostrinae* is a promising candidate for controlling the European corn borer (Hassan 1994; Wang et al. 1997; Wang and Ferro 1998; B. Wang and D. Ferro, unpublished data).

Temperature affects the activity of enzymes, the properties of cell membrane as well as other physiochemical activities, and consequently the development and behavior of organisms. Longevity and oviposition duration for *T. pretiosum* and *T. cacaoposi* were negatively correlated with temperature between 18 and 33°C, averaging from 14.0 to 4.0 d and 11.0 to 3.9 d, respectively, for *T. pretiosum*, and 2.9 to 1.4 d and 2.6 to 1.2 d, respectively, for *T. cacaoposi* (Navarro and Marcato 1997). The mean longevity for *T. turkestanica* Meyer ranged from 32 d at 15°C to just 2.3 d at 30°C, and the mean fecundity was 40 eggs at 30°C and 67–82 eggs at 15–25°C (Hansen and Jensen 2002). Haile et al. (2002) studied the development, survival, and progeny production of *T. bournieri* Pintureau & Babault, *T. sp. nr. muanzai* Schulten & Feijen, *T. evanescens* Westwood, and *T. chilonis* Ishii at four constant temperatures (13, 18, 25, 24°C), and found that *T. bournieri* and

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T. sp. nr. mwanzai failed to complete development at 13°C. The lower temperature thresholds for development and duration in degree days were 8.83°C and 188 for *T. chilonis* and 9.23°C and 192 for *T. evanescens*. *T. ostriniae* adults can only survive for 1–2.5 d between 20 and 35°C without supplemental nutrition (Zhang et al. 1983) and 3–8 d with 20% sucrose solution (Gou 1986). Almost 90% of female eggs are laid during the first 2 d after emergence (Qian et al. 1984). In addition, *T. ostriniae* prefers to parasitize newly oviposited host eggs (B. Wang, unpublished data). Accurate estimation of the development of *Trichogramma* species such as *T. ostriniae* is therefore crucial in biological controls of its host. This can be done using models. Several models have been proposed and used for the temperature-dependent development of insects. One of the earlier models is the linear day-degree model ($K = D [T - C]$). In this model, K is the thermal constant for the completion of the development of a specific stage or generation, D is the time required for the completion of development at temperature T , and C is the threshold temperature, below which no development occurs.

The linear model is easy to use, and the two estimated parameters are biologically meaningful. Therefore, it has been used for many years over the linear portion of the growth curve. However, the linear relationship only applies to the development rate between certain ranges of temperature for a given species. Therefore, nonlinear models were proposed for modeling the nonlinear growth found at high and low temperatures. Among the nonlinear models, the logistic equation proposed by Davidson (1942, 1944) and the Sigmoid equation used by Stinner et al. (1974) were criticized for their drawbacks at higher temperatures (Logan et al. 1976, Wagner et al. 1984). The Logan model (Logan et al. 1976), which combined two exponential equations to describe development rates at intermediate and high temperatures, has been found overestimating growth at low temperatures (Hilbert and Logan 1983). The model suggested by Sharpe and DeMichele (1977), although employing biophysical concepts, has been detected to overestimate insect growth at low and high lethal temperatures (Hilbert and Logan 1983, Gould and Elkinton 1990). The model is also poorly suited for nonlinear regression. Modification of the model by Schoolfield et al. (1981) makes the parameters biologically interpretable in addition to its fit for nonlinear regression. The model provided by Hilbert and Logan (1983) can be written as

$$R = b_1 \left(\frac{(T - b_2)^2}{(T - b_2)^2 + b_5^2} \right) - e^{(-b_3 + T - b_2)/b_4},$$

in which R is the development rate at temperature T ; b_1 is the rate of temperature-dependent, physiological process at base temperature b_2 ; b_3 is the lethal maximum temperature; b_4 is the temperature range between the developmental maximum and b_3 ; and b_5 is a empirical "shape" parameter that controls the inflection point of the sigmoid curve. This model has

been shown to provide good fits for the growth of several insects (Ferro et al. 1985, Roltsch et al. 1990). More satisfactory parameter evaluation can be obtained by using the observed time other than the modified form of rate in least-square-error of nonlinear regression (Kramer et al. 1991).

The effect of temperature on the development of *T. ostriniae* has been studied by several researchers (Zhang et al. 1983, Qian et al. 1984, Gou 1986). However, these studies either did not provide important information as to where the tested population originated and how it was maintained or did not perform suitable statistical analyses. Hence, whether their results can be applied to the introduced population is questionable because different colonies of *Trichogramma* may have significant behavioral and biological differences (Pak 1986, Smith and Hubbes 1986, Pak et al. 1986, 1990, Pavlik 1993).

A common problem of biological control using *Trichogramma* spp. are the declines in quality of laboratory-reared colonies of the wasps. Genetic processes such as drift and selection that could cause decreases in the field performance of laboratory-reared insects have been a continuing concern in biological control and mass-rearing projects (Machauer 1976, Roush 1990, Roush and Hopper 1995). Losey and Calvin (1995) reported lower number of emergence, and zero to low parasitization efficiency of four commercially produced species of *Trichogramma*. Studies have shown that continuous rearing of *T. maidis* Pintureau et Voegelé on factitious hosts may result in quality decline of the reared strains (Bigler et al. 1988, Bigler 1994, van Bergeijk et al. 1989), and thus egg parasitism of the target pests in the field. No comparable study has been conducted for *T. ostriniae*. The objectives of this study consisted of both the temperature-dependent development and comparison of oviposition behaviors of *T. ostriniae* reared on different hosts for several generations.

Materials and Methods

Parasitoid and Hosts. *T. ostriniae* were reared on either the eggs of the rice moth, *Corcyra cephalonica* (Stainton), or the eggs of the Asian corn borer, *O. furnacalis* (its native host). *C. cephalonica* larvae were reared on a wheat bran-soybean flour mixture (Zhu and Xie 1983, Zhang et al. 1991) at $27 \pm 1^\circ\text{C}$ and 75% R.H. Eggs (<24 h old) of *C. cephalonica* were sterilized by UV radiation (15 W, 50 cm from light source for 30 min). *O. furnacalis* larvae were reared at $25 \pm 1^\circ\text{C}$ and 80% R.H. on a semiartificial diet, as described by Du et al. (1985). *T. ostriniae* were reared from *O. furnacalis* eggs collected from the field in Jilin province of China.

The experiment included the following studies for *T. ostriniae*: 1) temperature-dependent development; 2) the effects of temperature on the success of parasitism, percentage of emergence from the parasitized eggs; and sex rate of different wasps (offspring); and 3) oviposition behaviors of female wasps reared on different hosts.

Temperature-Dependent Growth. Five female wasps, 48–72 h old, were placed into a glass vial (length 15 cm, diameter 3 cm) containing one *O. furnacalis* egg mass (50–70 eggs per mass) and held at $24 \pm 1^\circ\text{C}$. After 4 h, the wasps were removed and the parasitized eggs were placed in chambers held at one of the following temperatures: 17, 20, 24, 28, 30, and 33°C . There were 15 replications for each of the above-mentioned temperatures. The vials were examined once every 6–8 h, and the sex and number of adults that emerged were recorded at the time of emergence. This procedure was replicated 15 times for each temperature. The wasps used for this experiment were reared for seven generations on *O. furnacalis*, and then for three generations on *C. cephalonica*.

In our experiment, it is likely that the temperature range did not reach the low and high region of the development of *T. ostriniae*. Therefore, all the previously mentioned models except for the logistic equation provided a reasonable fit to the data using SigmaPlot (Jandel Corporation 1994, version 2.0). All models were reparameterized as time models by inverting the equations on both sides. In addition, the linear day-degree model was rearranged to $D = K/(T - C)$, because D is the outcome of the experiment, which was actually recorded. By this rearrangement, the model is no longer linear. However, the outcome parameters are still biologically important. We used the average number of hours needed for the species to complete development from egg deposition to adult emergence. However, this method is valid only when the number of the wasps that emerged from the hour the first wasp emerged to the hour the last wasp emerged at a temperature distributed exponentially. This exponentiality was checked by comparing, ΔH , the mean of the hours minus the minimum hours needed for development, with its standard deviation (SD). A property of the exponential distribution is that the mean is equal to the standard deviation. Therefore, if the number of wasps emerged per unit time (hours) was distributed exponentially, then we would expect the two sample values (ΔH and SD) to be approximately the same. The results did indicate that the data exhibit exponential distribution.

All the models were compared for their goodness of fitting the observed values. The criterion used was the residual sum of squares, $RSS_m^2 = \sum (X_f - X_o)^2$, where X_f is the model fitted value and X_o is the observed mean time needed for the wasp to complete the development at each temperature. The smaller the RSS_m^2 is, the better the model fits to the data.

The Effects of Temperature on Successful Parasitism, Wasp Emergence, and Sex Ratio. Wasps from generations 1, 2, 6, and 7 for *T. ostriniae* reared continuously on *O. furnacalis*, and wasps for *T. ostriniae* reared on *O. furnacalis* for three generations and then on *C. cephalonica* for 1, 4, and 6 generations were used in this study. Chambers were maintained at a photoperiod of 16:8 (L:D) h and 75% R.H. and at the following temperatures: 17, 20, 24, 28, 30, 33°C . Five fertilized female wasps (48–72 h old) were placed into a glass tube (length 15 cm and diameter 3 cm) con-

taining one *O. furnacalis* egg mass (50–70 eggs per mass). The tube was then placed into the chamber, and the wasps were removed from the tube after 24 h. This procedure was replicated 15 times for each temperature per generation. The number of parasitized eggs, number of viable and nonviable host eggs, and the number and sex of wasps that emerged were recorded.

Logistic regression models (Hosmer and Lemeshow 1989) were used for testing whether temperature and rearing hosts had any effects on successful parasitism of *O. furnacalis* eggs, the rate of emergence of the parasitized eggs, and sex ratios of emerged wasps. Dummy variables were assigned to each of the independent variables, which are temperatures (six temperatures, thus five dummies) and generations (seven generations, thus six dummies). The dependent variables analyzed each time were the rate of eggs parasitized, the number of wasps emerged from individual parasitized eggs, and the sex ratio of the emerged wasps.

Oviposition Behavior. The repertoire of behaviors associated with oviposition were characterized and observed for the different generations to detect whether there is any changes in oviposition behavior. An inexperienced female wasp (24–48 h old) was placed into a well (depth 5 mm and diameter 17 mm) containing an egg mass of 20 Asian corn borer eggs. The well was covered with a glass coverslip. Behaviors were observed through a dissecting scope with the well illuminated by a fiber optics light. The number and length of time allocated to the following behaviors were recorded: 1) drumming on host eggs with antennae, and 2) ovipositing into host eggs (including drilling into host eggs and probing host contents with ovipositor and egg deposition). Each wasp was left in the well for 15 min, allowing the wasp to acclimate for the first 5 min with observations made over the last 10 min. The number of eggs laid per host egg and the sex of the offspring were recorded. At least 10 wasps were observed for each generation tested.

Wasps of *T. ostriniae* from generations 1, 2, 6, and 7 reared continuously on *O. furnacalis*, and wasps of *T. ostriniae* reared on *O. furnacalis* for 3 generations and then on *C. cephalonica* for 1, 2, 4, and 6 generations were tested.

The oviposition behavior among different generations of *T. ostriniae* wasps was compared by using one-way analysis of variance (ANOVA), and then the Tukey test for multiple comparisons among different generations was used to rank means.

Results and Discussion

Temperature-Dependent Development. Optional development occurred at temperature from 28 to 33°C for both sexes. At these temperatures, it took ≈ 7 d for *T. ostriniae* to complete from egg to adult emergence. It took ≈ 9 , 14, and 20 d at 24, 20, and 17°C for the development, respectively. Our results varied from that reported for the temperature-dependent development of *T. ostriniae* by Qian et al. (1984) and Gou

(1986). Qian et al. (1984) reported that it took 12.5 d when reared on *Attacus sp.*, 11.6 d on *Dendrolimi spp.*, and 10.1 d on *Agrotis ypsilon* (Rotterberg). Gou (1986) reported that it took 10 d at 25°C for *T. ostriniae* to complete a generation when reared on the rice moth. Two factors may account for the differences. The first is the origin of the test population. Populations of the same species from different niches may have evolved for local environmental conditions. Therefore, the development rates may vary from one population to another (Wang and Zhang 1988). In addition, different host eggs may have different thickness and nutritional values to *T. ostriniae*, and consequently affected both the post embryonic development of *T. ostriniae* inside the host egg and the time it needed for development and to get out of the host egg.

The comparison for the fit of the six models to the data yields the following results: the residue sum of squares (unit: day²) is 1.37 for the Sigmoid model (Stinner et al. 1974); 1.34 for the $D = K/(T - C)$ model; 1.00 for the Quadratic model, $D = aX^2 + bX + c$ (where X is the temperature; a , b , and c are parameter to be estimated); 0.75 for the modified Sharpe and DeMichele model (Schoolfield et al. 1981); 0.72 for the Logan model (Logan et al. 1976); and 0.68 for the Hilbert and Logan model (Hilbert and Logan 1983). While all models seem to fit the data quite well, the Hilbert and Logan model had the lowest RSS_m value. However, this model, which requires the estimation of five parameters, is quite complex and may be necessary only in the situation such as for building simulation model in which precise estimation from each module is essential. The values of the five estimated parameters are $b_1 = 0.29 \pm 0.01$, $b_2 = 8.00 \pm 0.09$, $b_3 = 36.92 \pm 1.17$, $b_4 = 5 \pm 0.37$, and $b_5 = 20.12 \pm 0.18$. These parameters, especially b_2 , b_3 , and b_4 , are quite reasonable to what we have observed for *T. ostriniae*. The transformed day-degree model, although yielding a comparatively higher value of RSS_m , may still be very useful when precise estimation is not required. From the nonlinear regression analysis, the base temperature and thermal total is $10.71 \pm 0.39^\circ\text{C}$ and 130.36 ± 6.47 day-degrees, respectively. Therefore, the equation becomes $130.36 = D(T - 10.71)$.

Development of *T. ostriniae* occurred over a relatively wide temperature range, which is characteristic of insects found in temperate areas in which there can be a relatively wide fluctuation in temperatures from one day to the next.

The Effects of Temperature on Successful Parasitism, Wasp Emergence, and Sex Ratio. There were some differences between the different temperatures and between generations for percentage of parasitism. The Wald's P values for the following temperature-related dummy variables were all higher than 0.05, except for *Itemp* 33 (temperature 33°C versus 17°C), which was 0.03. For instance, *Itemp* 20 (temperature 20°C versus 17°C) was 0.784; *Itemp* 24 (temperature 24°C versus 17°C) was 0.353; *Itemp* 28 (temperature 28°C versus 17°C) was 0.987; and *Itemp* 30 (temperature 30°C versus 17°C) was 0.932. This means percentage of parasitism at 33°C was significantly lower

Table 1. % (mean \pm SD) *O. furnacalis* eggs parasitized by different generations of *T. ostriniae* at different temperatures

Gen. ^a	17°C	20°C	24°C	28°C	30°C	33°C
OF ₁	24 \pm 17	59 \pm 28	59 \pm 23	59 \pm 31	—	23 \pm 23
OF ₂	26 \pm 9	25 \pm 22	42 \pm 36	31 \pm 30	27 \pm 31	23 \pm 21
OF ₆	36 \pm 22	60 \pm 16	65 \pm 25	59 \pm 22	44 \pm 29	12 \pm 15
OF ₇	24 \pm 15	32 \pm 20	38 \pm 23	33 \pm 29	34 \pm 27	16 \pm 16
F ₃₊₁	34 \pm 20	60 \pm 25	64 \pm 29	74 \pm 26	69 \pm 16	10 \pm 13
F ₃₊₄	61 \pm 25	69 \pm 22	68 \pm 21	62 \pm 29	47 \pm 23	41 \pm 29
F ₃₊₆	58 \pm 25	69 \pm 25	58 \pm 12	61 \pm 31	56 \pm 27	48 \pm 28

^a Gen., generation tested; OF_x, reared on *O. furnacalis* for x generations; F_{x+y}, reared on *O. furnacalis* for x generations and then on *C. cephalonica* for y generations.

than at other temperatures, and there were no differences among the levels of parasitism at the other temperatures. The Wald's P values for the following generation-related dummy variables are 0.117 for *Igen* 2 (OF₂ versus OF₁), 0.671 for *Igen* 3 (OF₆ versus OF₁), 0.056 for *Igen* 4 (OF₇ versus OF₁), 0.932 for *Igen* 5 (F₃₊₁ versus OF₁), 0.146 for *Igen* 6 (F₃₊₄ versus OF₁), and 0.906 for *Igen* 7 (F₃₊₆ versus OF₁). Therefore, there was not much difference between generations, except for generation OF₇, which had a marginal P value when compared with OF₁.

In general, there were no statistical differences for the number of wasps that emerged from each egg or the proportion of females produced for each generation tested at different temperatures. The variability between replicates was too great to show any statistical differences. The percentage of parasitism ranged from a low of 10% at 33°C and a high of 69% at 20°C, and ranged from 25 to 69% from 20 to 28°C (Table 1). The number of wasps that emerged per host egg ranged from 0.3 at 24°C and 33°C to 1.51 at 28°C (Table 2). The proportion of females produced per egg mass ranged from 0.62 to 0.86 for the different temperatures and generations (Table 3).

Except for generation OF₇ and at temperature 33°C, there was no apparent difference among generations in their response to the different temperatures based on the parameters observed. The levels of parasitism for the different generations of *T. ostriniae* that had been reared on *C. cephalonica* were the same as those reared on *O. furnacalis* when each was exposed to *O. furnacalis* eggs. The number of wasps emerging per

Table 2. No. (mean \pm SD) *T. ostriniae* wasps that emerged per parasitized *O. furnacalis* egg for different generations and temperatures

Gen. ^a	17°C	20°C	24°C	28°C	30°C	33°C
OF ₁	1.2 \pm 0.7	1.4 \pm 0.6	1.1 \pm 0.3	1.5 \pm 0.5	—	0.7 \pm 0.5
OF ₂	0.6 \pm 0.3	1.3 \pm 0.6	1.3 \pm 0.7	1.2 \pm 0.4	1.0 \pm 0.6	0.8 \pm 0.5
OF ₆	0.5 \pm 0.4	1.0 \pm 0.2	1.6 \pm 0.9	1.2 \pm 0.4	1.0 \pm 0.3	0.6 \pm 0.4
OF ₇	1.1 \pm 0.7	1.2 \pm 0.5	0.3 \pm 0.2	1.1 \pm 0.7	1.2 \pm 0.5	0.7 \pm 0.5
F ₃₊₁	0.9 \pm 0.7	1.3 \pm 0.4	1.1 \pm 0.5	1.4 \pm 0.3	1.3 \pm 0.2	0.3 \pm 0.3
F ₃₊₄	1.0 \pm 0.2	1.1 \pm 0.4	0.4 \pm 0.3	1.2 \pm 0.5	1.0 \pm 0.4	1.1 \pm 0.7
F ₃₊₆	1.0 \pm 0.3	1.3 \pm 0.6	0.6 \pm 0.6	1.1 \pm 0.5	1.0 \pm 0.3	1.2 \pm 0.6

^a Gen., generation tested; OF_x, reared on *O. furnacalis* for x generations; F_{x+y}, reared on *O. furnacalis* for x generations and then on *C. cephalonica* for y generations.

Table 3. % (mean \pm SD) female *T. ostriniae* wasps that emerged from parasitized *O. furnacalis* eggs for different generations and temperatures

Gen ^a .	17°C	20°C	24°C	28°C	30°C	33°C
OF ₁	78 \pm 43	72 \pm 25	86 \pm 10	78 \pm 13	—	83 \pm 31
OF ₂	87 \pm 12	83 \pm 38	75 \pm 40	90 \pm 26	83 \pm 36	93 \pm 49
OF ₆	73 \pm 46	70 \pm 15	63 \pm 37	67 \pm 43	82 \pm 30	81 \pm 56
OF ₇	73 \pm 46	70 \pm 15	63 \pm 37	67 \pm 43	82 \pm 30	81 \pm 56
F ₃₊₁	58 \pm 47	78 \pm 23	83 \pm 25	85 \pm 10	87 \pm 6	97 \pm 64
F ₃₊₄	76 \pm 41	65 \pm 9	66 \pm 14	60 \pm 11	82 \pm 14	71 \pm 49
F ₃₊₆	62 \pm 23	62 \pm 30	62 \pm 49	72 \pm 37	86 \pm 26	78 \pm 26

^a Gen, generation tested; OF_x, reared on *O. furnacalis* for x generations; F_{x+y}, reared on *O. furnacalis* for x generations and then on *C. cephalonica* for y generations.

egg was the same as for all generations tested. The proportion of females produced for each treatment was the same across generations. These data would indicate that *T. ostriniae* is capable of successfully foraging for host eggs over a relatively wide temperature range. Again this is very reasonable for a parasitoid that exists in the northern temperate areas of China, where early season (late May) temperatures are in the mid-teens and can exceed 35°C in midsummer.

Oviposition Behavior. There were some differences (ANOVA; $F = 4.49$; $df = 7, 72$; $P < 0.01$) among generations for the number of seconds each wasp spent drumming (Table 4). However, the values did not demonstrate any clear trend based on generations tested. Part of the reason may be the high variability of the drumming behavior among individuals. The marginal difference (ANOVA; $F = 2.12$; $df = 7, 72$; $P = 0.052$) exhibited among generations for the number of seconds each wasp spent ovipositing came from the difference between generations F₃₊₄ and F₃₊₆. Although we do not have an explicit explanation to this result, the higher variability among individuals may again account partially for this phenomenon. This indicates that large number of replicates is needed for further evaluation of oviposition behaviors of *T. os-*

triniae. For the duration of the wasp spent drumming and ovipositing, readers should not judge the wasp's quality solely based on the value of the two parameters. During the experiment, we found that, for a successful parasitization, a female wasp usually spent 20–30 s drumming and 60–80 s ovipositing. This would indicate that only generations F₃₊₄ and F₃₊₆ behaved a little differently from the other generations. There were some subtle differences between generations in the proportion of time spent ovipositing while on an egg. For the 10-min observation period, no more than a little over 2 min of the wasp's time was spent in association with a host egg. There were no discernible differences in the behaviors associated with oviposition for the different generations, whether the wasps were reared continuously on *O. furnacalis* or *C. cephalonica*.

In summary, *T. ostriniae* was successfully reared under laboratory conditions on its native host, *O. furnacalis*, and on a factitious host, *C. cephalonica*. Generally, there were no apparent differences in wasp behaviors associated with oviposition for the different generations tested. However, there appeared to be a gradual decrease in the number of eggs parasitized per day per wasp as the number of generations in colony increased. There were no generational differences in the percentage of eggs parasitized, number of wasps that emerged per parasitized host egg, or the proportion of females produced as a function of temperature (17–33°C). These laboratory studies would indicate that *T. ostriniae* can be reared in mass for several generations either on the target host *O. furnacalis* or on the factitious host *C. cephalonica*, and if proper quality control is maintained, still produce wasps that can parasitize the target pest. These studies do not address any questions about how these wasps would respond to field conditions, but do provide important background information for mass production.

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Table 4. Oviposition behavior (mean \pm SD) of different generations of inexperienced female *T. ostriniae* wasps when *O. furnacalis* eggs were the host

Gen ^a .	D ^b	O	DT	OT
OF ₁	19.6ab ^c	78.6ab	0.37ab	0.18a
OF ₂	22.9ab	52.2ab	0.54ab	0.01a
OF ₆	22.3ab	52.2ab	0.63b	0.13a
OF ₇	30.0b	81.6ab	0.25a	0.22ab
F ₃₊₁	24.9b	67.2ab	0.28ac	0.41b
F ₃₊₂	25.1ab	82.9ab	0.36ab	0.15a
F ₃₊₄	10.3a	35.5a	0.55bc	0.11a
F ₃₊₆	26.4b	105.9b	0.25a	0.08a

^a Gen, generation tested; OF, reared on *O. furnacalis* for x generations; F_{x+y}, reared on *O. furnacalis* for x generations and then on *C. cephalonica* for y generations.

^b D, time spending drumming in seconds; O, time spending ovipositing in seconds; DT, proportion of time drumming while on egg; OT, proportion of time ovipositing while on egg for 10 min observation.

^c Within a column, means followed by the same letter are not significantly different ($P > 0.05$; Tukey test).

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